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Egg retention in wild-caught *Python bivittatus* in the Greater Everglades Ecosystem, Florida, USA

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Retention of eggs in oviducts beyond the normal oviposition period is a common problem for captive reptiles, but the occurrence of egg retention in wild populations is largely unknown. The Burmese python (*Python [molurus] bivittatus*; Kühl 1820) is an oviparous snake native to south-eastern Asia that is now established in southern Florida. From 2011–2019, invasive Burmese pythons were opportunistically removed from Everglades National Park and Big Cypress National Preserve, humanely euthanised, and necropsied to determine reproductive condition. A total of 258 females of reproductive size were found to exhibit various stages of oviposition which generally aligned with purported annual reproductive timing. However, we encountered five pythons during the post-ovulatory period (Aug–Feb) showing signs of recent oviposition with retained eggs. Most of these cases comprised a small number of retained eggs, likely representing some portion of the total clutch. Because this condition is nearly absent in wild animal literature, our observations suggest retained eggs in wild snakes may be more common than previously assumed, possibly slowing or otherwise impacting population growth. However, we recognise that for an invasive species like the Burmese python in Florida, the egg retention rate may be higher in the non-native range compared to the native range due to maladaptation to novel habitats or environmental conditions. Additional research is needed to determine the exact causes of egg retention and investigate the implications for population dynamics on this and other snake species.

Keywords: invasive species, dystocia, snakes, Burmese, reproduction

INTRODUCTION

Egg retention, whereby eggs are held in oviducts beyond the normal oviposition period, is a common reproductive problem in captive reptiles, but reports on its occurrence in wild populations are scarce (Barten, 1985; DeNardo, 2006; Knotek, 2015; Di Girolamo & Selleri, 2017; Govendan et al., 2019). Issues of egg retention are thought to be caused by various factors including physical obstruction, physiological abnormalities, poor maternal body condition, or inadequate captive environmental conditions (DeNardo et al., 2000; DeNardo, 2006; Estrada et al., 2015; Efendić et al., 2017). Although squamates with varying reproductive strategies have occasionally exhibited egg retention (Hoffman, 1970; Lapasha et al., 1985; Plummer, 1996; Blackburn et al., 1998; Blazquez et al., 2000; Bel et al., 2015), the condition is most common in oviparous snakes and often accompanies dystocia (difficulty associated with birth or egg laying; Stahl, 2006). If a snake is incapable of passing eggs (dystocia), then the eggs remain inside the oviduct (egg retention).

Because these conditions sometimes lead to death in captive animals, reports of egg retention and dystocia from wild populations of reptiles are scarce, and the natural frequencies are generally unknown (Lapasha et al., 1985; Plummer, 1996; DeNardo et al., 2000; DeNardo, 2006). The impact on oviparous snake populations has the potential to be profound in long-lived species with individually high reproductive output. However, without close monitoring of robust numbers of wild individuals in a population or destructively sampling a cross section, cases of these conditions cannot be identified and documented.

The Burmese python (*Python [molurus] bivittatus*; Kühl 1820) is a large, oviparous snake native to south-eastern Asia (Murphy & Henderson, 1997), but is now an established invasive species across southern Florida, USA, including in Everglades National Park and Big Cypress National Preserve (Snow et al., 2007; Willson et al., 2011; Reed et al., 2012; McCleery et al., 2015). These invasive predators have multiple impacts including preying on imperiled species, pets, livestock, and commercially

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important species, outcompeting native predators, and acting as a pathogen or disease vector to native species (Reed & Rodda, 2009).

Although necessary to combat this threat, data on the breeding season across the Burmese pythons' broad native range is limited and varies widely (Van Mierop & Barnard, 1976). Hatchlings are usually seen in late July which places the oviposition period from late spring into early summer (Bhupathy & Vijayan 1989). In southern Florida, the breeding season extends from mid-December through mid-March, and female Burmese pythons appear to oviposit from May through June (Harvey et al., 2008; Reed & Rodda, 2009). Female Burmese pythons are highly fecund, with clutch sizes frequently exceeding 50 eggs in southern Florida (Harvey et al., 2008; Reed & Rodda, 2009; Krysko et al., 2012). However, very little is known about nesting frequency or success in this invasive population and, to the best of our knowledge, we are the first to report egg retention in any (native or invasive) wild-caught Burmese pythons. Because egg retention in female snakes can have fatal consequences or cause sterility in captivity (Ross & Marzek, 1990), it follows that the condition may have deleterious effects on the wild population dynamics. Therefore, focused studies on nesting and clutch success may inform population size, structure, and growth; these are important considerations for conservationists and land managers involved with this invasive species' impacts on native species. These studies may also help to better understand oviparous snakes in general, such as those that are threatened or the focus of conservation efforts.

METHODS

As part of mitigation and removal strategies, Burmese pythons are actively captured from Everglades National Park, Big Cypress National Preserve, and other areas in the Greater Everglades Ecosystem. Some of these specimens are surrendered to the National Park Service (NPS) and U.S. Geological Survey (USGS) for study and are humanely euthanised using a penetrating captive bolt followed by pithing according to American Veterinary Medical Association (AVMA) guidelines (AVMA 2020). Nearly 60 % of these surrendered animals are then necropsied to obtain morphometrics and determine reproductive condition, diet, and other research variables of interest.

For this study we necropsied 258 female Burmese pythons ≥ 210 cm total body length [TL, $\sim \geq 186$ cm snout-vent length] captured from southern Florida throughout the year, from 2011–2019. Although the sexually mature size for female Burmese pythons in their native range has been reported as 260 cm TL or greater (Wall, 1921; Lederer, 1956; Reed & Rodda, 2009), after necropsying many snakes we found the smallest female containing eggs measured 210 cm. Willson et al. (2014) also encountered a small female (210 cm TL) that contained eggs. Of the 258 females we necropsied, 149 were captured during the post-ovulatory period (Aug–Feb). Nineteen of 149 exhibited oviducts that had not undergone complete involution (post-ovulatory shrinkage or recovery). The

hypertrophied oviducts suggest those 19 females had recently oviposited with five of the individuals exhibiting egg retention during post-ovulatory months.

RESULTS

Herein, we examine the cases of egg retention observed in the five females showing signs of recent oviposition and report on possible etiologies and implications (Table 1). Python 1 contained two eggs in the cranial portion of the right oviduct. Python 2 was emaciated with depleted fat bodies and had three retained eggs, two in the right oviduct and one in the left (Table 1a & 1b). Python 3 had five retained eggs that appeared irregular with highly wrinkled shells (Table 1c & 1d). Python 4 had developing primary follicles and 35 densely-packed retained eggs that appeared to have solidified (Table 1e). Python 5 was emaciated with depleted fat bodies, had three retained eggs in the right oviduct, and contained an unidentified mass near the vent. It is worth noting that in four of the five cases only a small number of eggs were retained ($n \leq 5$) when clutches from wild Burmese pythons in Florida can contain 62–87 eggs (Krysko et al., 2012, Josimovich et al., 2021, Currylow et al., 2022).

DISCUSSION

In documented cases of dystocia and egg retention, female snakes were usually able to oviposit the majority of their clutch (Barten, 1985; Stahl, 2006), suggesting that the four females with the smaller numbers of eggs had previously oviposited the majority of the clutch. Although the etiologies for our reported cases of egg retention are unknown, evidence at necropsy indicated that these pythons could have experienced dystocia. As mentioned above, dystocia is generally classified into two types, obstructive and non-obstructive. Obstructive dystocia is usually caused by physical abnormalities in or around the female's reproductive tract or by eggs of abnormal shape or size (DeNardo, 2006). It may also result when a small female (e.g. below normal reproductive size) carries average-sized eggs (i.e. the eggs are too large to pass through the oviducts or vent). Non-obstructive dystocia includes that caused by poor physical condition of the mother (e.g. underdeveloped musculature), metabolic imbalances, infections, hormonal interference, nutritional deficiencies, dehydration, or inadequate environmental conditions (DeNardo, 2006; Estrada et al., 2015; Efendić et al., 2017).

As described for Python 5, a mass was discovered near the vent that may have caused an obstructive dystocia and resulted in promoting retention of the three eggs. However, this explanation lacks merit with the assumption that the female was able to pass the rest of the clutch, unless these few remaining eggs were larger or misshapen. Two of the other pythons (Python 1, 210 cm TL and Python 3, 246 cm TL) were at or near the smallest reported reproductive size for this species (210 cm TL; Willson et al., 2014) and it is therefore possible that those two females lacked the size, energy

Table 1. Capture date, snout-vent length (SVL), total length (TL), number of retained eggs, and photo references of invasive Burmese pythons (*Python bivittatus*) after being removed from the wild in the Greater Everglades Ecosystem, Florida, USA. Capture dates are outside the typical oviposition season of May–June.

	Capture date	SVL (cm)	TL (cm)	# Retained eggs	Photo reference
Python 1	August 2011	216	246	2	None taken
Python 2	August 2014	274	312	3	Figures 1a & 1b
Python 3	December 2016	186	210	5	Figures 1c & 1d
Python 4	August 2019	421	472	35	Figure 1e
Python 5	September 2019	247	282	3	None taken

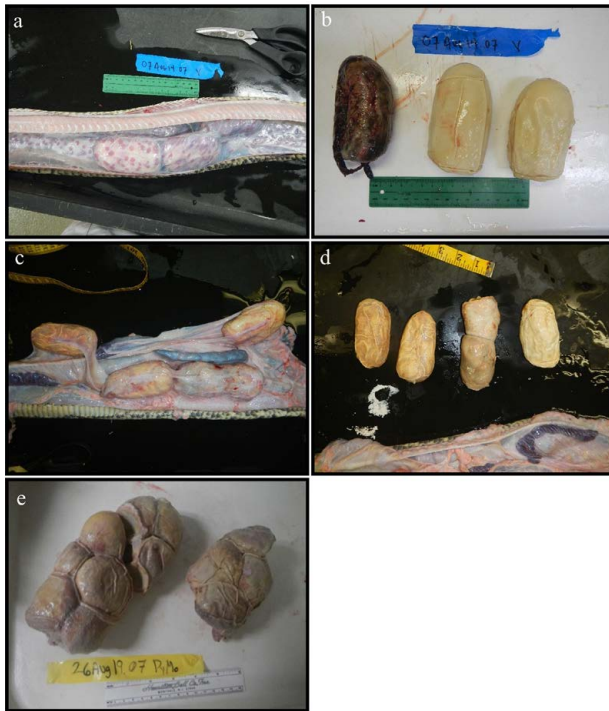


Figure 1. Photos of wild-caught, invasive Burmese pythons (*Python bivittatus*) individuals removed from Everglades National Park, Florida USA. **a)** Three retained eggs in situ within the right oviduct and extremely depleted fat bodies (red dots) in the fascia and **b)** removed from the oviduct of Python 2 **c)** Five retained eggs in situ within the oviduct and **d)** removed from the oviduct of Python 3. This was the smallest animal we detected with this condition. Note the apparent shrinkage of the eggs as evidenced by the significant wrinkling of their surfaces in d). **e)** A subset of the 35 densely-packed and solidified eggs found in Python 4. This animal showed no other abnormalities at necropsy.

resource accumulation and/or muscle development to successfully oviposit the larger eggs. However, without more information on the relation between female size and egg size and extended specimen observation, it is difficult to determine causes. Python 2 exhibited poor body condition which could support the hypothesis of a non-obstructive dystocia due to some concurrent condition, or that extended retention of the partial clutch negatively affected its health.

Python 4 was the only python to contain a large

number of retained eggs ($n = 35$). Difficulty laying a full clutch, or the majority of a clutch, is documented in captive Burmese pythons (Govendan et al., 2019). Python 4 had no other observed physical abnormalities at necropsy, but we cannot rule out obstructive causes since the original size and shape of the eggs could not be determined. The snake exhibited normal body condition so the high number of retained eggs did not appear to adversely affect the snake during the unknown time of retention. While primary follicles were observed developing in the ovaries, it is possible that the retained eggs could have adversely affected any future reproduction or caused sterility of the female (Ross & Marzek, 1990).

These five cases represent atypical timing for Burmese python oviposition in southern Florida (i.e. Aug–Feb), and all retained eggs were wrinkled or otherwise appeared shrunken in size (Fig. 1). Wrinkled or shrunken appearance is likely caused by water reabsorption from the eggs (Blackburn et al., 1998), but eventual expulsion is far more likely than complete resorption in squamates (Hoffman, 1970; Blackburn, 1998; Blackburn et al., 1998; Blackburn et al., 2003). Barring obstructive complications it is possible that the retained eggs could have been extruded later. However, because nearly all published records of egg retention involve captive animals with subsequent chemically induced or surgical egg removal, successful extrusion or subsequent death rates are not known (Barten, 1985; DeNardo, 2006; Knotek, 2015; Di Girolamo & Selleri, 2017). Retained fertile eggs eventually die and may decompose, which can cause infections, uterine rupture and coelomitis (Ross & Marzek, 1990). Unfertilised retained eggs, although less prone to decomposition complications, can affect future reproduction (Ross & Marzek, 1990). All retained eggs have the potential to cause sterility and death (Ross & Marzek, 1990). It is worth noting that in the other instances of egg retention reported in wild oviparous snakes, one snake underwent surgery and was later released while two others died (Lapasha et al., 1985; Plummer, 1996; DeNardo et al., 2000).

There is limited evidence that snakes may live for several years with retained eggs with no adverse health effects (Ross & Marzek, 1990). We do not know if any of the wild pythons could have later expelled the retained eggs on their own nor whether retained eggs would

affect survival of free-ranging pythons. While it is thought that dystocia in wild reptiles is an infrequent occurrence (DeNardo et al., 2000; DeNardo, 2006), our observations suggest it may be more common than previously assumed or reported with 12 % of the adult females captured and necropsied (n = 258) containing eggs. Of those gravid females, 17 % (n = 5 of 30) had retained eggs that were found during atypical timing for oviposition in southern Florida. This suggests a surprisingly high egg retention rate considering the purported risk of sterility or death.

Here we present the first cross-sectional data on this condition in a wild population of invasive snakes. It is unclear if egg retention in wild snakes is more common than previously believed, or if these invasive snakes are experiencing a higher retention rate due to maladaptation to their relatively novel environmental conditions. However, determining the probable causes and natural occurrence rates of egg retention in wild snake species would require additional effort. A clearer understanding of the possible causes or impacts of egg retention is needed to evaluate its impact on population dynamics of both invasive and native snake species, especially those of special concern for conservation.

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Authors' Contribution

Funding provision: Robert N. Reed, Bryan G. Falk, Andrea F. Currylow, Amy A. Yackel Adams. Research conceptualisation: Andrea F. Currylow, Gretchen E. Anderson. Data collection: Bryan G. Falk, Amy A. Yackel Adams, Robert N. Reed. Data analysis: Andrea F. Currylow, Gretchen E. Anderson. Subject expertise: Frank N. Ridgley, Robert N. Reed. Writing original draft: Gretchen E. Anderson, Andrea F. Currylow, Jillian J. Josimovich. Reviewing and editing: All authors contributed to improving the manuscript.

Ethical Statement

All research was conducted under full compliance with federal and state legislation. Euthanasia methods were developed in consultation with the National Park Service Wildlife Health Team and all euthanasia was humanely performed.

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